

## Polarized and specular reflectance variation with leaf surface features

Lois Grant, C. S. T. Daughtry and V. C. Vanderbilt

Grant, L., Daughtry, C. S. T. and Vanderbilt, V. C. 1993. Polarized and specular reflectance variation with leaf surface features. – *Physiol. Plant.* 88: 1–9.

The linearly polarized reflectance from a leaf depends on the characteristics of the leaf surface. In the present study the leaf reflectance of a number of plant species with varying surface characteristics was measured at the Brewster angle with a polarization photometer having 5 visible and near-infrared wavelength bands. We found that all leaf surfaces polarized incident light. Differences among species could be explained by variation in surface features. The results support our hypothesis that the polarized light is reflected by the leaf surface, not by its interior. Two mechanisms appeared responsible for the linearly polarized reflectance: (1) specular reflectance and (2) surface particle scattering. In most cases, large values of linearly polarized reflectance could be attributed to specular reflectance from the leaf surface. Attribution required knowledge of the optical dimensions of features on the leaf surface.

**Key words** – Cuticle, leaf surface, light, polarization, reflectance, scattering, specular reflectance.

L. Grant (corresponding author), 823 Forest Drive, Wooster, OH 44691, USA; C. S. T. Daughtry, USDA, ARS, Remote Sensing Research Laboratory, BARC-West, Beltsville, MD 20705, USA; V. C. Vanderbilt, MS 242-4, Ames Research Center, Moffett Field, CA 94035, USA.

### Introduction

A leaf surface, like any dielectric boundary, scatters and transmits light. In some view directions, the surface reflection may be so large that fields of sunflower, corn, sorghum, wheat and grass appear white instead of green. The white light visually overwhelms the much smaller amounts of green light scattered by the interior of the leaves (Grant et al. 1987a).

The surface reflection from the leaf may be in part a specular reflection whose magnitude may be estimated from polarization measurements of the reflected light. We have proposed that polarized light reflected by a leaf contains information about the leaf surface – information independent of that already identified in light diffusely reflected from the interior of the leaves (Vanderbilt et al. 1985a, Grant et al. 1987a).

In the present paper we study the effect of surface features on leaf reflectance by examining the polarized reflectance of the leaves of plant species exhibiting various surface characteristics.

### Specular reflectance

At near-normal incident angles, specular reflectance from the leaf surface is presumed minimal (T. R. Sinclair, 1968, M.S. Thesis, Purdue Univ., West Lafayette, IN, USA) and often negligible (Knipling 1970). Interpretation of reflectance differences has assumed that diffusely scattered light from the bulk of the leaf tissue primarily determines reflectance (Gausman et al. 1970, 1973). Grant (1987) has reviewed the diffuse and specular characteristics of leaf reflectance.

At large, off-normal angles of incidence, leaf reflectance increases (Gates and Tanspohn 1952), possibly due to the effects of specular reflection (Shul'gin and Khazanov 1961). Leaf reflectance is intermediate between that of a perfectly diffuse and a perfectly specular reflector (Breece and Holmes 1971, Brakke et al. 1989, Sarto et al. 1989, Walter-Shea and Norman 1989), which suggests it is the sum of diffuse and specular components. The diffuse component is nonpolarized, varies little with changing angles and emanates from the

Received 16 November, 1992



interior of the leaf (Shul'gin and Khazanov 1961, Shul'gin and Moldau 1964). The nondiffuse component is polarized, emanates from the leaf surface and is spread about the specular direction (Rvachev and Guminetskii 1966, Vanderbilt et al. 1985a). Specular reflection appears to be the principal light scattering process polarizing reflected light, although scattering by surface roughness features can play a role (Vanderbilt et al. 1985a). The leaf surface roughness determines the angular spread of the polarized, specular reflectance lobe because leaves appear capable of specularly reflecting light in all directions (Rvachev and Guminetskii 1966, Woolley 1971, Vanderbilt et al. 1985a).

The amount of light specularly reflected by a leaf varies with species (Grant et al. 1983, 1987a,b, McClendon 1984). McClendon (1984) noted that the variation in specular reflectance is greater than that of diffuse reflection. Visibly shiny leaves tend to have higher specular reflectance than matte leaves (Shul'gin and Khazanov 1961), although leaves which have no shiny appearance can still specularly reflect light (McClendon 1984). Leaves with sparsely distributed hairs can specularly reflect more light than glabrous leaves and some highly pubescent leaves may be strong specular reflectors (McClendon 1984). Thus the presence or absence of hairs does not serve as a predictor of specular reflectance.

The specular reflectance of a leaf surface could be predicted with the Fresnel equations (Hecht and Zajac 1976) if the surface were optically smooth, which is unlikely. More typically, leaf surfaces exhibit roughness features which, when compared with the wavelength of light, range in size from very large to small. Small particles and features on the leaf surface will scatter light away from the specular direction (the direction in which the angle of incidence equals the angle of reflection) (Fung 1983). Large features such as venation control the amount of light scattered into the specular direction (Fung 1983).

The nondiffuse, specular component of leaf reflectance can be determined with a photodetector equipped to measure the polarization of the reflected light. The polarized reflectance equals the specular reflectance when the angles of incidence and reflectance both equal the Brewster angle, approximately 55° (Rvachev and Guminetskii 1966).

## Materials and methods

### Plant materials

We estimated leaf reflectance twice on both the adaxial and abaxial sides of each of 6, fully expanded, attached leaves of each plant species measured in situ during the summer and fall of 1983. Data of agronomic and weed species *Glycine max* Merr., *Helianthus annuus* L., *Sorghum bicolor* L., *Zea mays* L., *Abutilon theophrasti* Medic., *Asclepias syriaca* L., *Chenopodium album* L.

and *Solanum ptycanthum* Dun. were collected at the Purdue Agronomy Farm, West Lafayette, IN.

Data of forest species *Acer saccharum* Marsh., common variety, *Acer saccharum* Marsh., variety native to Indiana, Illinois and Missouri, *Quercus borealis* Michx., *Quercus prinus* L., *Quercus velutina* L. and *Ulmus americana* L. were collected at Prophet's Rock Reservation, Battle Ground, IN. Data of vegetable species *Cucurbita pepo* L. and *Lycopersicon esculentum* Mill. were collected from a private garden in West Lafayette, IN. Data of the potted plant species *Caladium bicolor* Vent. and *Gynura aurantiaca* D.C. were collected in the laboratory.

### Reflectance measurements

Reflectance measurements were collected with a portable polarization photometer (Fig. 1) (Vanderbilt and Grant 1985) which allows nondestructive estimation of leaf reflectance at approximately the Brewster angle (55 degrees from normal) in 5 wavelength bands in the visible and near-infrared spectrum centered at 450, 500, 550, 650 and 730 nm with a half power band width of 70 nm.

To estimate reflectance, we calibrated the photosensor response to a sample  $V_{\text{sample}}$ , by measuring (1) a painted BaSO<sub>4</sub> standard,  $V_{\text{std}}$ , of known reflectance,  $R_{\text{std}}$  and (2) the dark level of the instrument,  $V_{\text{dark}}$ . The bidirectional reflectance factor (Nicodemus et al. 1977) of the sample expressed as a percent is:

$$\frac{V_{\text{sample}} - V_{\text{dark}}}{V_{\text{std}} - V_{\text{dark}}} \times R_{\text{std}} \times 100\% \quad (1)$$

Each observation consisted of a pair of reflectance factors,  $R_{\text{max}}$  and  $R_{\text{min}}$ , representing, respectively, the maximum and minimum amounts of light transmitted by the polarization analyzer. From these values, the following variables were calculated:

$$R = \frac{R_{\text{max}} + R_{\text{min}}}{2.0} \quad (2)$$

$$R_Q = \frac{R_{\text{max}} - R_{\text{min}}}{2.0} \quad (3)$$

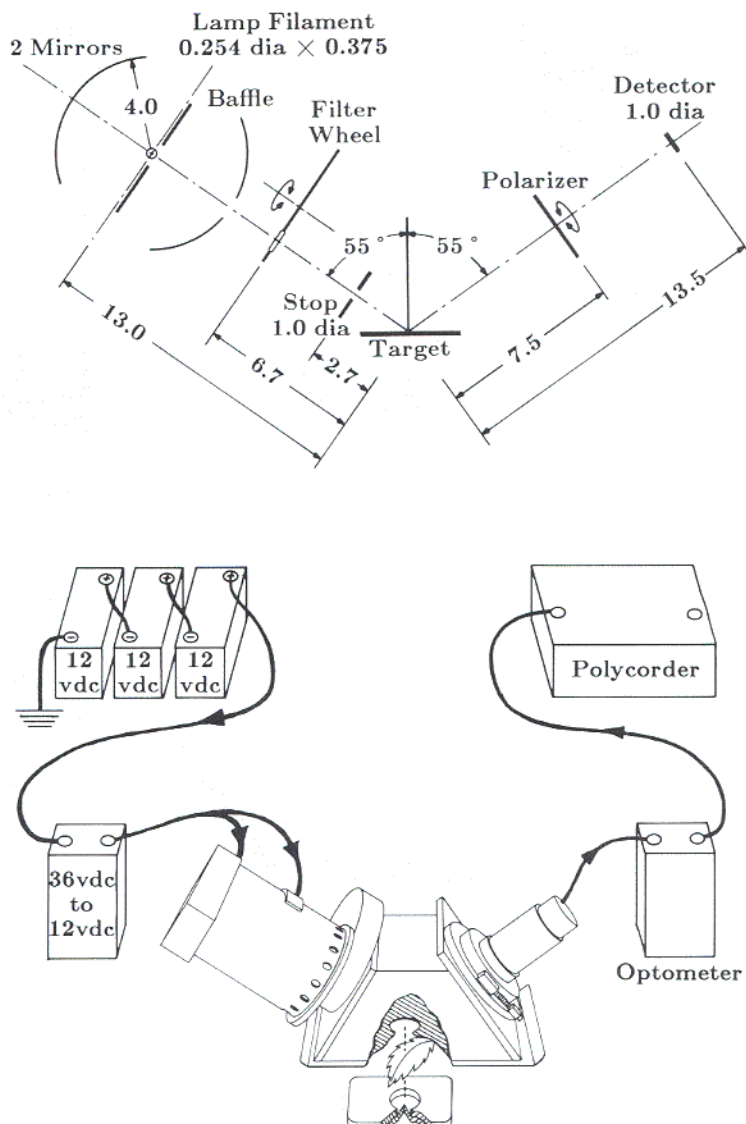
$$R_N = R - R_Q \quad (4)$$

$$P = \frac{R_Q}{R} \times 100\% \quad (5)$$

$R$  is the bidirectional reflectance factor of the leaf illuminated and measured both at angles of 55°, approximately the Brewster angle. The polarized component



Fig. 1. With the portable polarization photometer, the polarized bidirectional reflectance factor may be determined in situ at angles of incidence and reflectance of  $55^\circ$ , approximately the Brewster angle.



$R_O$  of the reflectance factor equals the specular reflectance of the leaf provided surface particles negligibly polarize incident light. The nonpolarized component  $R_N$  of the reflectance factor equals the diffuse reflectance of the leaf. The degree of polarization,  $P$ , is the percentage of the reflected light that is polarized.

## Results and discussion

### Origin of polarized reflectance

The results (Fig. 2A,B, Tab. 1) show that the linearly polarized part  $R_O$  of the leaf reflectance factor in the visible and near-infrared wavelength regions appears unaffected by cellular pigments in each leaf. Statistical tests show there is no significant change in  $R_O$  with wavelength; spectrally,  $R_O$  is flat. The results (Fig.

2C,D) show that the nonpolarized part  $R_N$  of leaf reflectance varies spectrally according to the constituent pigments in each leaf. How can light reflected by a leaf not display at least some evidence of interaction with leaf pigments, especially pigments with a spectral presence so evident in  $R_N$ ? The answer appears to be that the polarized part of the reflected light never entered the leaf tissue to interact with the leaf pigments. These results support our hypothesis that  $R_O$  represents light reflected at the leaf surface (Grant et al. 1983, 1987a, Vanderbilt et al. 1985a,b).

### Effect of large surface features

The large range of  $R_O$  among these species (Fig. 2A,B) manifests the variation of such large features as pubescence and surface undulations, features with dimen-

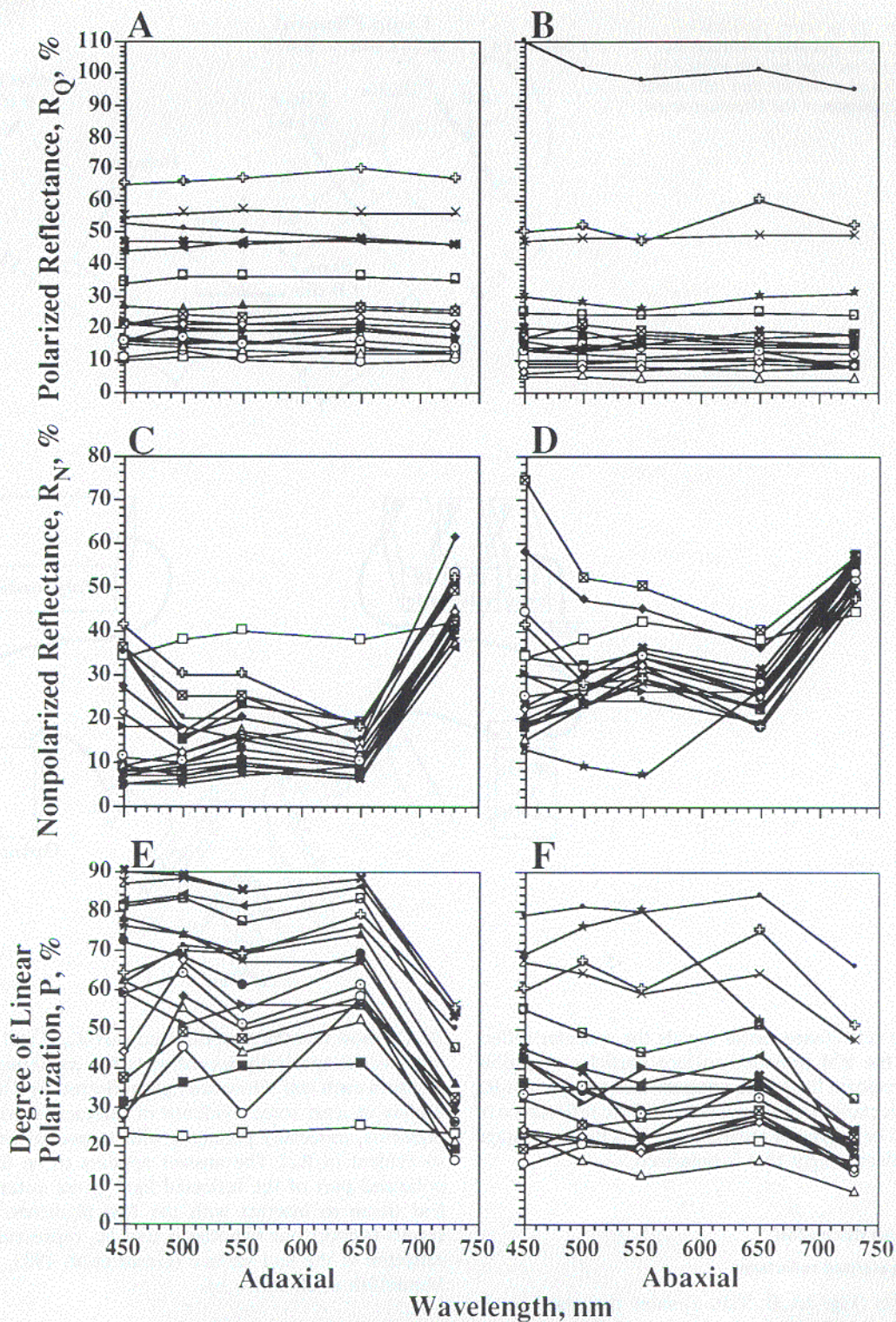


Fig. 2. Polarized reflectance,  $R_Q$ , nonpolarized diffuse reflectance,  $R_N$ , and degree of polarization,  $P$ , from the adaxial and abaxial surfaces of leaves of 18 species were measured spectrally at the Brewster angle. Data are means of two measurements of 6 leaves per species. Symbols corresponding to each species are listed in Tab. 1, which also lists a standard deviation, calculated from data collected at 650 nm but representative of standard deviations at other wavelengths.



Tab. 1. Polarized reflectance,  $R_O$ , nonpolarized diffuse reflectance,  $R_N$ , and degree of polarization,  $P$ , from the adaxial and abaxial surfaces of leaves of 18 species were measured at the Brewster angle at a wavelength of 650 nm. Data are means,  $\bar{x}$ , and standard deviations,  $s$ , of two measurements of 6 leaves per species. Species correspond to symbols in Fig. 2 (percent).

Symbol	Species	Adaxial						Abaxial					
		$R_O$		$R_N$		$P$		$R_O$		$R_N$		$P$	
		$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$
■	<i>Abutilon theophrasti</i>	14	5	19	5	41	7	16	5	29	4	35	7
●	<i>Acer saccharum</i> , common	21	6	9	6	69	7	14	2	25	4	36	4
▲	<i>Acer saccharum</i> , Indiana	27	1	9	1	74	6	10	2	26	4	28	3
◆	<i>Asclepias syriaca</i>	20	2	15	3	58	5	13	4	36	5	27	5
□	<i>Caladium bicolor</i>	13	3	38	6	25	3	11	5	38	7	21	5
○	<i>Chenopodium album</i>	9	4	14	4	58	5	7	2	18	1	28	6
△	<i>Cucurbita pepo</i>	12	2	13	3	52	6	4	1	22	3	16	4
◇	<i>Glycine max</i>	23	6	11	3	67	7	9	2	25	4	26	5
★	<i>Gynura aurantiaca</i>	19	4	9	1	67	5	30	6	27	2	52	5
⊠	<i>Helianthus annuus</i>	26	9	19	4	56	7	17	6	40	9	29	9
⊙	<i>Lycopersicon esculentum</i>	16	3	10	3	61	6	13	5	28	7	32	3
▣	<i>Quercus borealis</i>	36	13	7	1	83	6	25	10	22	2	51	11
◄	<i>Quercus prinus</i>	47	18	7	1	86	5	15	4	22	2	43	5
×	<i>Quercus velutina</i>	56	22	7	1	88	6	49	24	23	6	64	16
►	<i>Solanum pycnanthum</i>	19	4	19	3	56	5	15	4	26	6	37	4
⊕	<i>Sorghum bicolor</i>	70	20	18	9	79	7	60	23	18	5	75	8
×	<i>Ulmus americana</i>	48	14	6	1	88	3	19	5	31	3	38	4
●	<i>Zea mays</i>	48	16	15	4	76	4	101	14	19	5	84	4

sions many times the wavelength of light. Hairs specularly reflect light and obscure the leaf surface to both illumination and view, processes which modify the specular reflection from the leaf. The results (Fig. 2A,B) show that leaves displaying somewhat pubescent to densely pubescent adaxial surfaces have values of adaxial  $R_O$  less than 25%, except the common variety of *Acer saccharum*. Sparsely pubescent or glabrous leaves have an adaxial  $R_O$  greater than 25%. Large values of  $R_O$  imply that much of the leaf surface is relatively flat, approximating a plane surface.

Adaxial  $R_O$ , except for one species, was greater than or equal to the abaxial  $R_O$ , because the abaxial surface tended to be rougher. For example, the adaxial leaf surfaces of *Quercus prinus* and *Acer saccharum* are both glabrous and *Asclepias syriaca*, is sparsely pubescent. In each case, the specular reflectance of the smooth adaxial surface is greater than that of the pubescent or densely pubescent (Bailey 1949, Petrides 1972) abaxial surface. The one exception is *Zea mays*, which rolls its leaves to form tight vertical cylinders in response to drought. We propose that the large abaxial  $R_O$  (= 101%) of *Z. mays* is a further adaptation to drought stress. [Unlike the bidirectional reflectance factor (BRF) of a perfectly diffuse surface, the BRF of a specular surface, viewed in the specular direction, may exceed 100%. A specular surface redirects the incident light into just the specular direction rather than into all directions as would a hypothetical, perfectly diffuse, perfectly white standard. The bidirectional reflectance factor of the surface is the large amount of light measured in the specular direction divided by the comparatively small amount of light which would be reflected by

the hypothetical standard viewed in the same direction.] When corn leaves roll, sunlight obliquely hits the highly reflective abaxial surface rather than the less reflective adaxial leaf surface, decreasing the energy load on the plant. If our hypothesis is correct, corn provides an example where the specularly reflected light plays an important role in the energy balance of the plant (Gates et al. 1965).

Besides pubescence, leaf surface undulations can affect specular reflectance. For example, *Gynura aurantiaca*, with densely pubescent leaf surfaces, had an adaxial  $R_O$  = 19% (supporting the 25% rule); however, the abaxial  $R_O$  = 30% (violating the 25% rule). The hairs on both the adaxial and abaxial surfaces are similar, but the convex abaxial topographical undulations redirect a significant part of the abaxial specular reflection toward the sensor.

Our conclusion that, in most cases, adaxial  $R_O \geq$  abaxial  $R_O$ , is opposite to that of McClendon (1984), a dichotomy attributable to measurement methods. McClendon illuminated leaves at 60° and measured them at two angles, defining the reflectance at 0° as the diffuse reflectance and that at 60° as the specular reflectance. A leaf surface potentially can reflect light specularly in all directions, including the angles 0° and 60° (Vanderbilt et al. 1985). McClendon's estimates of reflectance at 0° possibly included both diffusely and specularly reflected light, as would his estimates for the reflectance at 60°.

For most dicotyledonous leaves, the value of the adaxial diffuse reflection,  $R_N$  (Fig. 2C), is less than the abaxial  $R_N$  (Fig. 2D), a result in accord with that of Gausman et al. (1970, 1973). The greater specular re-



Tab. 2. Ratio of blue (450 nm) nonpolarized reflectance ( $R_N$ ) to red (650 nm) nonpolarized reflectance ( $R_N$ ) of leaves measured at the Brewster angle. Within each column, means with the same letter are not significantly different using Duncan's Multiple Range Test,  $\alpha = 0.05$  (dimensionless).

Adaxial		Abaxial	
Species	Mean	Species	Mean
<i>Chenopodium album</i>	2.36 a	<i>Chenopodium album</i>	2.39 a
<i>Helianthus annuus</i>	1.75 b	<i>Helianthus annuus</i>	1.81 a
<i>Abutilon theophrasti</i>	1.69 b	<i>Zea mays</i>	1.73 b
<i>Glycine max</i>	1.66 b	<i>Asclepias syriaca</i>	1.35 c
<i>Sorghum bicolor</i>	1.64 b	<i>Abutilon theophrasti</i>	1.33 c
<i>Zea mays</i>	1.61 bc	<i>Sorghum bicolor</i>	1.11 cd
<i>Asclepias syriaca</i>	1.55 bc	<i>Quercus prinus</i>	0.93 de
<i>Quercus prinus</i>	1.26 cd	<i>Lycopersicon esculentum</i>	0.92 de
<i>Lycopersicon esculentum</i>	1.17 de	<i>Glycine max</i>	0.92 de
<i>Quercus velutina</i>	1.13 def	<i>Solanum pycnanthum</i>	0.90 de
<i>Solanum pycnanthum</i>	1.12 def	<i>Quercus velutina</i>	0.87 de
<i>Acer saccharum</i> , common	0.84 ef	<i>Quercus borealis</i>	0.83 e
<i>Ulmus americana</i>	0.79 ef	<i>Acer saccharum</i> , Indiana	0.78 e
<i>Acer saccharum</i> , Indiana	0.78 ef	<i>Ulmus americana</i>	0.75 e
<i>Quercus borealis</i>	0.75 f	<i>Acer saccharum</i> , common	0.74 e
<i>Cucurbita pepo</i>	0.75 f	<i>Cucurbita pepo</i>	0.68 e

flectance measured on the abaxial surface by McClen-  
don (1984) may be attributed to the greater diffuse  
reflectance of the abaxial surface.

#### Effect of small surface particles

Polarized reflectance,  $R_Q$ , cannot be attributable solely  
to specular reflectance, which is associated with rela-  
tively smooth surfaces. Mid-sized particles having di-  
mensions comparable to the wavelength of incident  
light also scatter and polarize light. Even though small,  
the amount of light scattered and polarized may be  
important for some species.

Our results suggest that another potential source of  
polarized light, scattering by sparsely distributed parti-  
cles having dimensions much smaller than the wave-  
length of the incident light, is not important among the  
species measured. Small particles scatter and polarize  
light preferentially in the blue wavelength region and,  
as already noted,  $R_Q$  of all measured species is spec-  
trally flat (Fig. 2A,B). This means no measurable  
amounts of light scattered by small particles contributed  
to  $R_Q$ , because polarized reflectance does not increase  
significantly toward the blue wavelengths.

The amount of light polarized through small particle  
scattering on the leaf surface appears unimportant, per-  
haps because the amount of light scattered by each  
particle is tiny and the amount scattered by the aggre-  
gate of particles, if sparsely distributed, is also tiny.  
When the surface particle density is sufficiently large  
that the scattered light is detectable, then the particles  
probably do not scatter that light independently of one  
another. The horizontal separation distance between  
particles on leaves displaying a bluish bloom is often less  
than a wavelength or two of light, less than its coher-  
ence length. The crystalline wax "particles" are at-

tached to the amorphous wax substrate, forming in ag-  
gregate a structure conceptually like a miniature an-  
tenna field in which photons interfere and multiply scat-  
ter. Large particle densities increase the likelihood that  
a photon polarized after one scattering will be randomly  
polarized after multiple successive scatterings, a process  
which decreases the polarization of the total reflected  
light.

Even if polarized small particle scattering appears  
unimportant, a blue/red ratio test (Gausman et al. 1973)  
of the nonpolarized reflectance  $R_N$  (Tab. 2) suggests  
that nonpolarized scattering by small features on the  
leaf surface is important for the leaves of some species.  
Use of the ratio technique assumes that green leaves  
reflect 70 to 90% of the radiation within the internal leaf  
structure in the blue region compared to that of red.  
(*Caladium bicolor* and *Gynura aurantiaca* are not in-  
cluded in Tab. 2 because their leaves are not primarily  
green.)

*Sorghum bicolor* leaves, which had the largest adaxial  
 $R_Q$  (Fig. 2A,B), display two types of epicuticular waxes  
overlaid upon a ridged venation pattern typical of a  
monocotyledonous leaf (Atkins and Hamilton 1982).  
On the adaxial surface, clusters of small wax flakes, 100  
to 160 nm by 210 to 1580 nm, are sparsely distributed  
and thus scatter little light. This suggests that specular  
reflection is the most important adaxial light scattering  
process and consequently  $R_Q$  should be large, which it  
is. On the abaxial surface, diffuse mid-size particle scat-  
tering appears important because wax filaments 500 to  
1250 nm in diameter and up to 14000 nm long densely  
cover the surface. It is unclear why abaxial  $R_Q$  is com-  
paratively large.

The adaxial, abaxial blue/red  $R_N$  ratios of *Sorghum  
bicolor* are 1.64 and 1.11, respectively (Tab. 2), suggest-  
ing that Rayleigh-sized particles do contribute to



adaxial reflectance, but contribute little to abaxial reflectance, a result which is in accordance with the optical dimensions of sorghum surface particles (Atkin and Hamilton 1982).

On *Chenopodium album* with the smallest  $R_0$  (Fig. 2A,B), vesicular hairs (small globules attached by a stem to the leaf surface) cover both the adaxial and abaxial surfaces of immature leaves, and collapse to a highly corrugated surface as the leaf matures (Brian and Cattlin 1968).  $R_0$  may be small because the corrugated areas tend to specularly spread incident light over a large range of directions rather than concentrating a specular lobe toward the sensor. Large-scale roughness can also spread the specular lobe at the surface of *Cucurbita pepo* which is rough, irregular and covered with small sharp specularly reflecting hairs (Bailey 1949). *Cucurbita pepo* has very low values of both  $R_0$  and the blue/red  $R_N$  ratio (Tab. 2), implying no small particle scattering.

Greater magnification (Taylor et al. 1981) of both surfaces of *C. album* reveals small, irregularly distributed, epicuticular wax platelets with average dimensions 200 by 1000 nm which can also serve to decrease  $R_0$ . The extremely high density and depth of the platelets covering the abaxial surface appears to preclude specular reflection from the underlying surface.

The blue/red ratios of *C. album*, 2.36 and 2.39 for the adaxial and abaxial surfaces, respectively (Tab. 2), are significantly greater than for any other species and suggest that small particle scattering affected the surface reflection. Again, the large ratio of blue/red  $R_N$  coupled with the spectral flatness of  $R_0$  shows that the scattering by small-sized particles is not polarized.

The nonpolarized reflectance  $R_N$  cannot be interpreted as emanating solely from the internal leaf structure. The results (Tab. 2) show that half of the species studied have adaxial particles which contributed to  $R_N$  but few species have abaxial particles contributing to  $R_N$ . This shows that knowledge of the optical characteristics of a leaf surface is essential for interpreting not only the polarized/specular reflectance, but the diffuse reflectance as well.

#### Significance of polarized/specular reflectance

The degree of polarization, Equation 5, includes information from two dissimilar sources, a fact which complicates data interpretation. The numerator  $R_0$  contains information about the leaf surface and is a leaf-dependent constant (Fig. 2A,B). The denominator  $R(\lambda) = R_0 + R_N(\lambda)$  contains information about the internal structure of the leaf in addition to the leaf surface and varies with wavelength as a function of the absorption spectra of the dominant leaf pigments. Thus, the degree of polarization  $P(\lambda)$  for a leaf may be written

$$P(\lambda) = 100\% \frac{R_0}{R_0 + R_N(\lambda)} = 100\% \frac{\{\text{constant}\}}{\{\text{constant}\} + R_N(\lambda)} = \frac{100\%}{1 + \frac{R_N(\lambda)}{\{\text{constant}\}}} \quad (6)$$

To simplify data interpretation, we prefer to report the polarized reflectance,  $R_0$ , rather than the degree of linear polarization,  $P$ .

The results (Fig. 2) show the spectral variation of  $P(\lambda)$  estimated from Equation 5. For any one species,  $P(\lambda)$  is small when  $R_N(\lambda)$  is large, as in the near-infrared spectral region, and large when  $R_N(\lambda)$  is small, as in the pigment-absorbing visible region. For example, values of  $R_N$  for *Caladium bicolor*, which appears white because it contains little light absorbing pigment, are relatively high throughout the visible spectrum. Conversely, the values of  $R_N$  are low for *Gynura aurantiaca* which contains both anthocyanin and chlorophyll. Similar results have been reported for green, red and white portions of *Coleus blumei* (Grant et al. 1987a). Values of  $R_N$  of chlorophyll-containing green leaves are low in the blue (450 nm) and red (650 nm) wavelengths and relatively high in the green (550 nm). In the infrared (730 nm), values of  $R_N$  are large for all plant species. In all these cases, the degree of polarization  $P$  of a leaf varies spectrally more or less as the absorption spectrum of the dominant pigments in the leaf.

If  $R_0$  is greater than  $R_N$ , then Equations 5 and 6 show that  $P$  will be greater than 50% and the surface properties will be the dominant factor determining leaf reflectance. If  $P$  approaches 100%, it will contain no information about the internal structure of the leaf. The results (Fig. 2E,F) show that for some species the polarized reflectance from the leaf surface may be the dominant factor determining leaf reflectance measured in photosynthetically active regions of the spectrum. This is illustrated by the results for the 650 nm wavelength band dominated by chlorophyll absorption in green leaves. For example, *Caladium bicolor*, which contains little chlorophyll or other light-absorbing pigments in this wavelength band, had a large value of  $R_N$  and the lowest value of  $P$ , 25% (Fig. 2E). The adaxial  $P$  of all other species except *Abutilon theophrasti* was greater than 50% (Fig. 2E), demonstrating that the polarized component was the dominant factor determining leaf reflectance at 650 nm for these species. For example,  $P$  equaled 58% for *Chenopodium album*, which exhibited the lowest  $R_0 = 9\%$  (Fig. 2A,B). This means the polarized reflectance, 9% accounted for 58% of the total light reflected by the leaf in the direction of the photodetector of the measurement system.

In the 730 nm near-infrared wavelength band, the nonpolarized diffuse reflectance  $R_N$  is controlled more



by scattering from the internal leaf structure than by pigment absorption, unlike in the visible wavelength region. As a result, values of  $R_N$  are higher than in the visible (Fig. 2C,D) and again mirror low values of  $P$ . Adaxial  $P$  ranged from 16% for *C. album* to 56% for *Quercus velutina* (Fig. 2E). Abaxial  $P$  ranged from 8% for *Cucurbita pepo* to 66% for *Zea mays* (Fig. 2F). Thus, depending on the species and direction of measurement, the polarized reflectance of the surface may be an important factor in determining leaf reflectance even in nonphotosynthetically active regions of the spectrum.

Values of  $R_0$  and  $P$  reported here pertain only to light both incident and reflected at the Brewster angle where specularly reflected light is completely, linearly polarized. At reflection angles away from the Brewster angle, polarization measurements can provide an underestimate of the amount of specularly reflected light.

## Conclusions

Light reflected by a leaf can be separated into two components with the aid of polarization measurements. One component originates at the surface of the leaf and contains no information about leaf pigments, while the other emanates primarily, but not entirely, from the interior leaf tissue. Its magnitude is determined by leaf pigments and other energy-absorbing metabolites. The variable of choice for performing the separation is the polarized component of the reflectance factor rather than the more traditional variable, the degree of linear polarization.

This conclusion, that linear polarization of visible and near-infrared light reflected by leaves is a first surface phenomenon unaffected by cellular pigments, metabolites and structure, is tentative and remains to be tested on a wider variety of species.

All measured species appear to polarize reflected light. Differences among species can be attributed to variations in leaf surface structures. Two mechanisms appear potentially responsible for polarized leaf reflectance: (1) specular reflectance and (2) scattering by surface particles with sizes comparable to light. Surface features much smaller than the wavelength of light scattered light but did not polarize it.

We propose that *Z. mays* exhibits a large abaxial  $R_0$  as an adaptation to drought stress, illustrating that the specularly reflected light may play an important role in the energy balance of the plant.

**Acknowledgement** – This research was performed at Purdue University, West Lafayette, IN 47907, USA, under a grant NAS5-269 from the National Aeronautics and Space Administration. Publication was supported by the NASA headquarters code SEPO3 program on remote sensing science to investigate the optical properties of leaves and plant canopies.

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